provided by the papillae and the highly vascularized nature of these papillae.

SUMMARY

1. Tests were performed on the snails, *Tegula funebralis* and *T. brunnea,* to determine the nature and quantity of their excretory products and the organs of excretion.

2. Standard colorimetric assays were used on homogenates prepared from the ctenidium, digestive gland, right and left kidneys. Total non-protein nitrogen, ammonia, urea, and uric acid were determined.

3. Uric acid was observed to be the major excretory product of these snails. It accounted for 11.8% to 76.6% of the total non-protein nitrogen in the right kidneys, the only organs where this waste product was detectable. Only slight traces of ammonia were found in the digestive gland, and no urea was present in the tissues tested.

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The Distribution and Movement of *Tegula funebralis* in the Intertidal Region of Monterey Bay, California

(Mollusca : Gastropoda)

BY

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(9 Text figures)

INTRODUCTION

Tegula funebralis (A. ADAMS, 1854) is very common along the west coast of California, although little work has been done on its intertidal distribution. Hewatt (1934) describes its distribution as between the plus one and plus five foot level above mean lower low water. Ricketts and Calvin (1962, pp. 352-355) put the population center at the three foot tide level. Neither reference describes the distribution extent along the intertidal region. We investigated *Tegula funebralis*' intertidal distribution and movement patterns in relation to certain biological and physical environmental factors. Before investigating movement patterns, we wanted an accurate, correlatable distribution analysis for several areas along Mussel Point, Pacific Grove, California. To do this, we collected information pertaining to numbers and size classes of this snail along with environmental data of the areas, such as vertical level of collection, algal covering, area configuration, substratum, and wave and current action. Factors that seem to

affect the distribution were then checked by exposing marked populations to these various conditions and observing the movements of the snails.

METHODOLOGY

We selected five areas along Mussel Point, each, as described below, representing a different environmental condition. In each area we marked the exact water level at low tide on a very calm day to give correlatable marks, whose height was then determined by use of existing benchmarks. At low tide a transect two meters wide was extended from shore to the minus two foot tide level in each area, and every *Tegula funebralis* within the transect was counted and measured for the largest basal diameter of the shell from the lip to the edge of the opposite side.

In order to investigate the movement patterns of *Tegula funebralis,* we put marked populations into areas which best represented the factor being tested and compared their movements with the movements of control groups in areas where the factor did not exist. A periodic position plot of the individuals within the population over time resulted in an overall movement pattern which, when compared with that of other populations, gave information on the effectiveness of certain factors in influencing population distribution.

POPULATION DISTRIBUTION

Area A is a rocky, open coastline with a heavy algal covering. It has no current movement though the outer rocks facing seawards receive heavy wave action.

Area B is a rocky, open coastline without an algal covering. It has no current movement though the entire profile receives the heaviest wave action of all five areas. Mussels and barnacles almost entirely cover the rock surfaces below the plus three foot tidal level, and all *Tegula funebralis* are found among these animals.

Area C is a semi-protected area with a heavy algal covering. The area has a light current flowing through it with a moderate wave surge.

Area D is a semi-protected area with a heavy algal covering. There is usually a moderate current flowing through it with a moderate wave surge, although the inner third

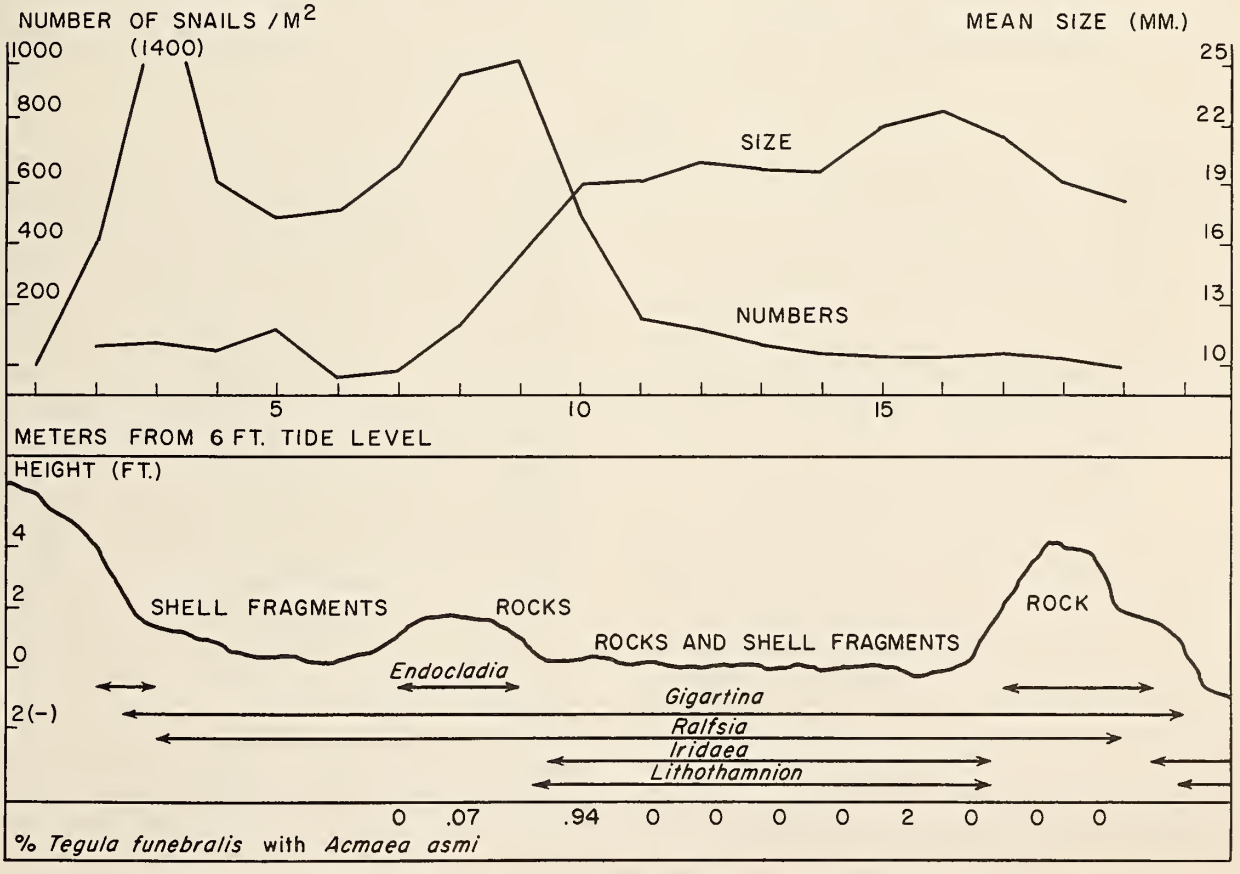

Figure 1: Distribution in numbers and size classes of *Tegula funebralis* in Area A

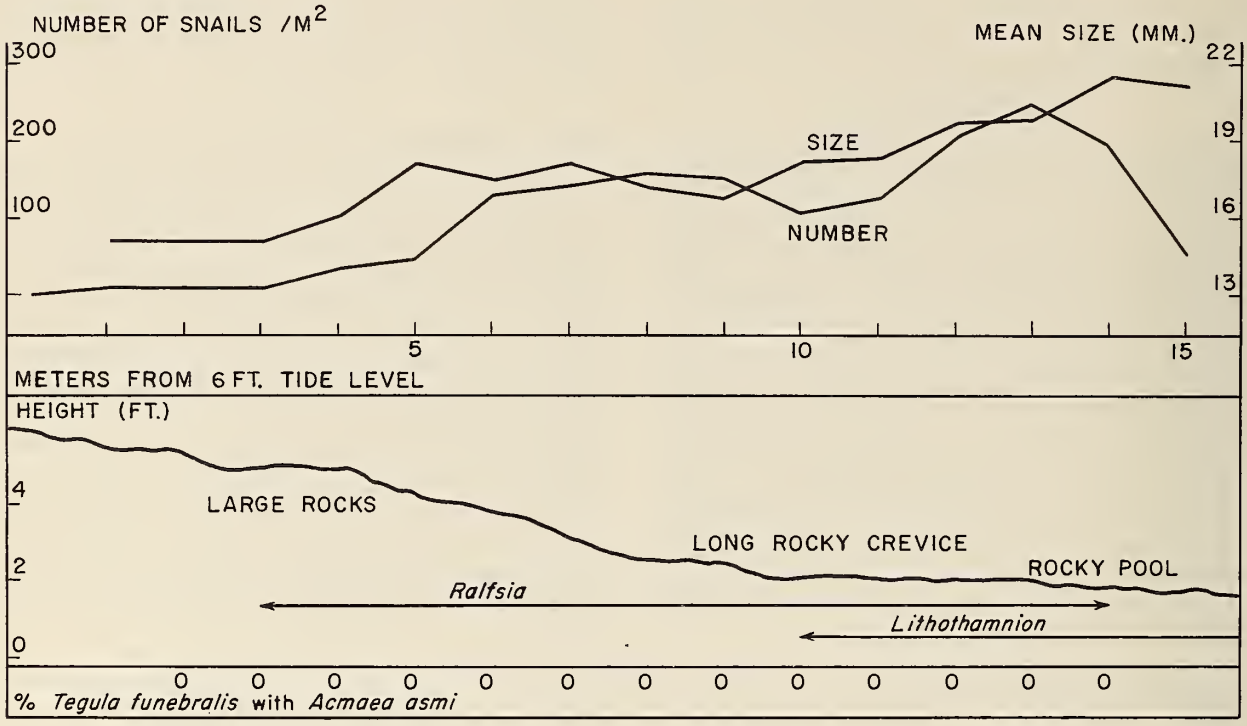

Figure 2: Distribution in numbers and size classes of *Tegula funebralis* in Area B

of this profile has relatively quiet water.

Area E is a protected area with a sparse algal covering. It has no current movement and little wave surge. Pools in this area are very crowded at low tide and some of the *Tegula funebralis* move about on the fine sand bottom of the pools. Only in these pools were the snails found to be grazing on dead algae, periodically cast up at high tide.

In all five areas *Tegula* tends to be clumped in places that have a sparse algal covering and usually is dispersed in areas of dense coverage.

DISCUSSION AND CONCLUSIONS

(Distribution)

The collecting of *Tegula funebralis* was done at low tide; small irregularities in population numbers due to substrate irregularities smooth out at high tide when the snails disperse from their clumps in the crevices. In plotting their distribution in relation to certain environmental factors, we found relationships which indicate that certain biological and physical factors may control population distribution.

The population density decreases as the amount of algal covering increases, indicating that population density depends to some extent on the amount of open rock surface available. Rocky areas which have little algal covering have a larger number of snails on them than a heavily covered rocky area. The reason for this distribution may be that rock surfaces provide the main food source for their grazing. Two notable exceptions are found, one in Area C at the twenty-eight meter mark (Fig. 3) where outer rocks are washed by heavy surge, reducing the density of snails in this area, and the other in Area D at the fifteen meter mark (Fig. 5) where a shell fragment substrate decreases the population density.

The mean size of the animals increases with the degree of algal covering. The larger snails are found in the heavy algal covering more often than in protected crevices.

Moderate current does not affect the *Tegula funebralis* distribution, as the higher densities found along rock faces bordering the channel in Area D at thirty-eight meters are similar to the densities found shoreward at four meters in quiet water (Fig. 5).

Population densities are reduced in areas of heavy water turbulence. Area B with its heavy surf is relatively barren of *Tegula funebralis* (Fig. 2). The outer rocks in Area C which receive heavy wave action are also sparsely

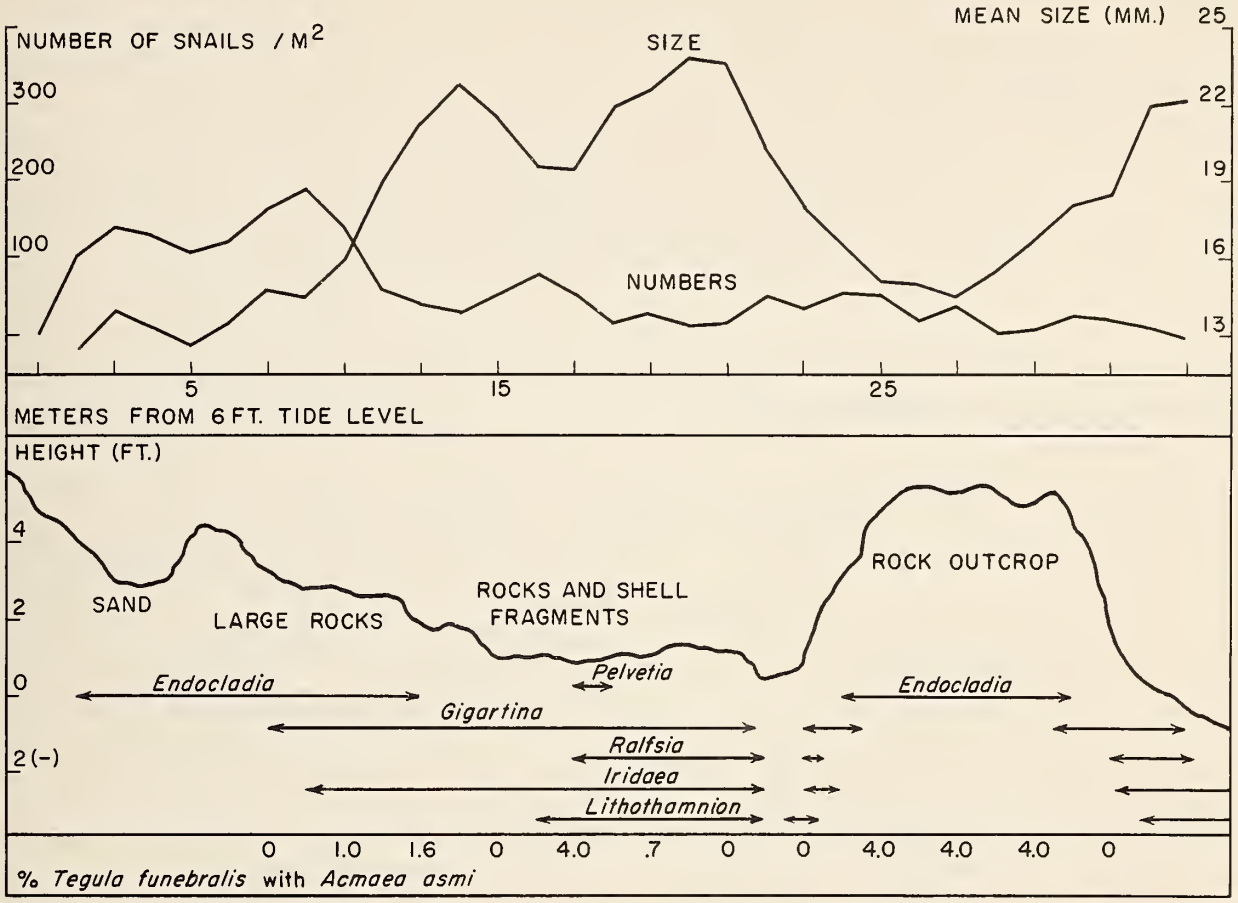

Figure 3: Distribution in numbers and size classes of *Tegula funebralis* in Area C

populated, while similar areas closer to shore in calmer water have higher densities of snails (Fig. 3).

Vertical height clearly affects the population density quite aside from the maximum height of zero feet and plus six feet (Fig. 8). Between these limits similar heights in different places show different numbers of individuals as found in Area A between seven and sixteen meters from shore (Fig. 1), in Area C between eleven and twenty-five meters (Fig. 3), and in Area D (Fig. 5). Different vertical heights having similar population densities are found in Area C twelve and twenty-seven meters from shore, in area D between forty-two and fifty-four meters, and in Area D between forty-two and fifty-four meters, and in Area E between five and nine meters (Fig. 4). The greatest population density is at the plus two to four foot tidal level (Fig. 8). The mean size of animals decreases with increase in the vertical height along the transects with the largest snails rarely found at the seaward edge of the transect (Fig. 7).

POPULATION MOVEMENTS

Population I (marked in the size classes 0-15 mm, 15-20 mm, and over 20 mm), was placed in Area D on outer rocks at the plus two foot tidal level. Water at high tide was turbulent with little current movement. This population was plotted for fifteen days (Fig. 9).

Population II (marked as in Population I), was placed in Area D on inner rocks at the plus three foot tidal level. Water at high tide was calm without current movement. This population was plotted for 19 days (Fig. 9).

Population III was placed in Area D at the plus three foot tidal level on an outer rock face bordering the current

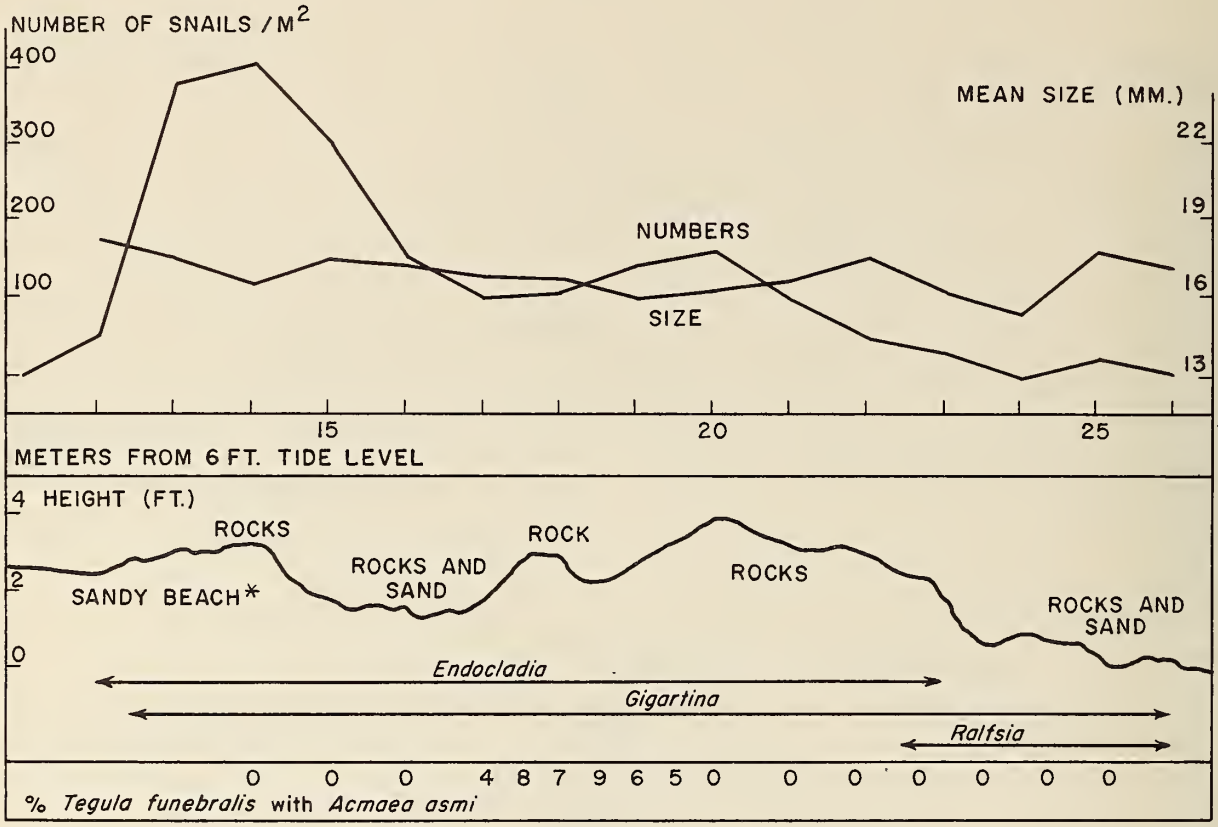

Figure 4: Distribution in numbers and size classes of *Tegula funebralis* in Area E (*sandy beach extends shoreward eleven meters to the plus six foot level)

channel. At high tide a moderate current runs through this channel. This population was plotted for fourteen days. After the first fourteen day study was completed, Population III was placed in the current channel at the minus one foot tidal level, directly out from the point of its original placement and was found after five days to have dispersed much as on the fifth day of the first period (Fig. 9).

Population IV, clustered under three rocks at the plus four foot tidal level, was marked and its vertical movement was followed during rising and falling tides over periods of 24 hours. During daylight hours at high tide, the population remained beneath the rocks with individuals rarely on rock tops. At night during high tides the population moved to the rock tops in large numbers. They moved up as soon after twilight as the tide permitted, in numbers dependent on the intensity of the moonlight. On bright moonlit nights the density on rock tops was half that found during dark overcast nights. During the low tide periods at night about four-fifths of the snails moved down; all snails moved down at the first light of dawn. On nights of heavy wave surge the numbers on the rock tops were one tenth those normally found on the rocks for dark nights. This vertical movement was noted at many places along Mussel Point.

Population V (two groups, one taken from the zero to plus one foot level and the other from the plus four to five foot level) was marked and placed at the plus two foot level in a crevice of a rock outcrop. The rocks extend from a sandy substrate at zero feet to plus seven feet. The two groups, plotted for fourteen days, showed no vertical or horizontal separation. However, sixteen individuals were found beyond four meters down current and only nine beyond this distance up current.

DISCUSSION AND CONCLUSIONS

(Movement)

Tegula funebralis moves up to rock tops during the night high tide, but not during the daylight high tides. The

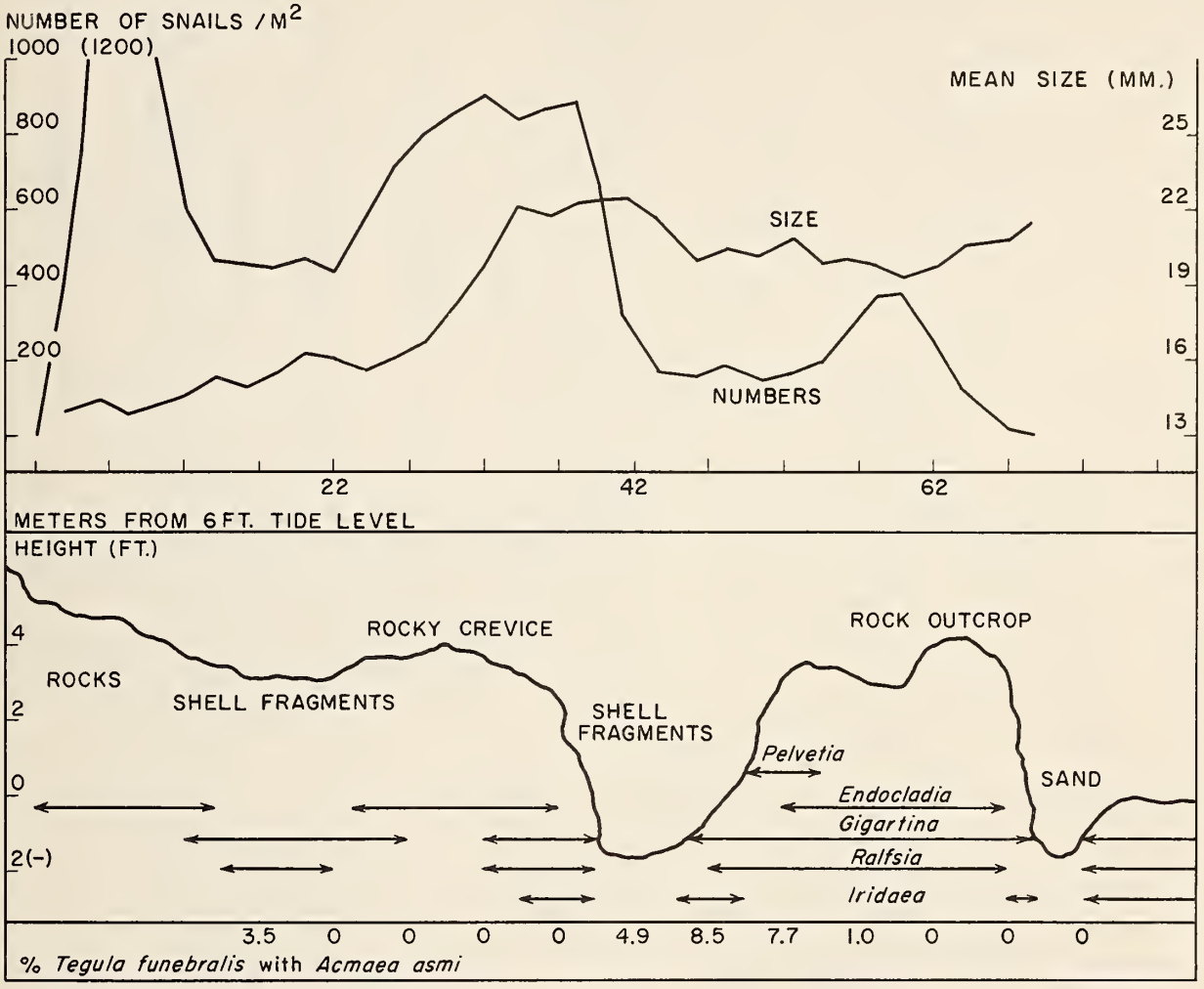

Figure 5: Distribution in numbers and size classes of *Tegula funebralis* in Area D

upward movement seems to be light-dependent with the threshold level inhibiting this movement at the light intensity of the full moon.

Tegula funebralis movements seem to be directed by water current to some extent, as slightly more of the individuals in Populations III and V were found down current than up current.

As shown by the movement of Population V, there seems to be no vertical specificity for *Tegula funebralis* but a random dispersal.

The movements of *Tegula funebralis* do not appear to differ with size; the three size classes were intermixed throughout the dispersal of Populations I and II.

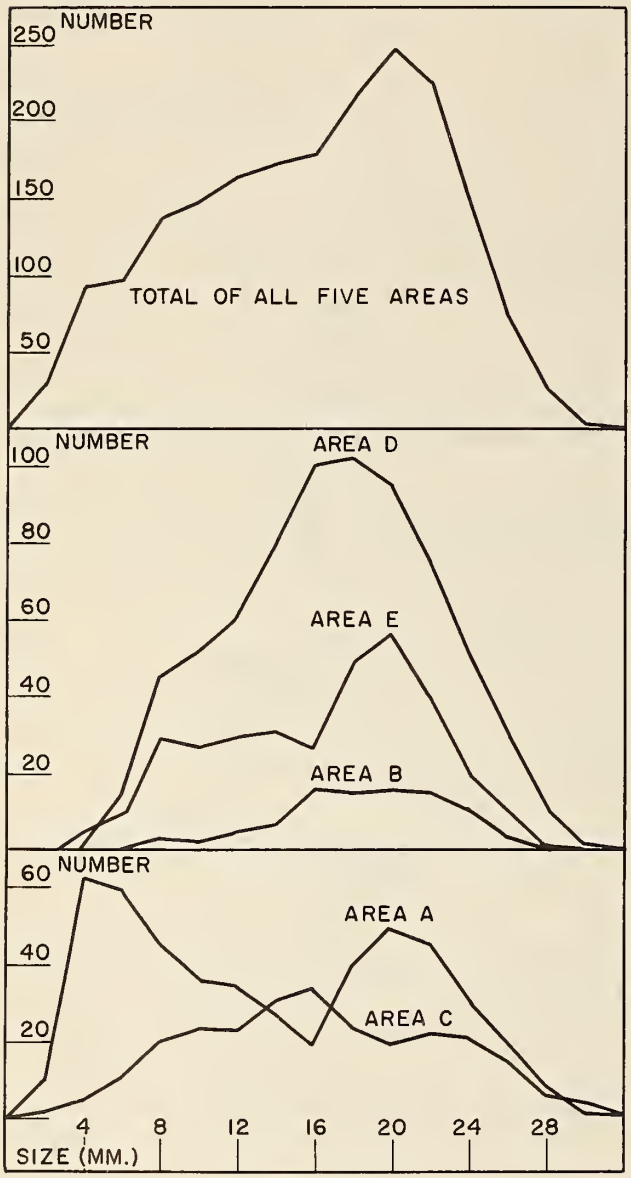

Figure 6: The relationship between numbers of animals and size classes for each of the five areas plus a total for all five areas

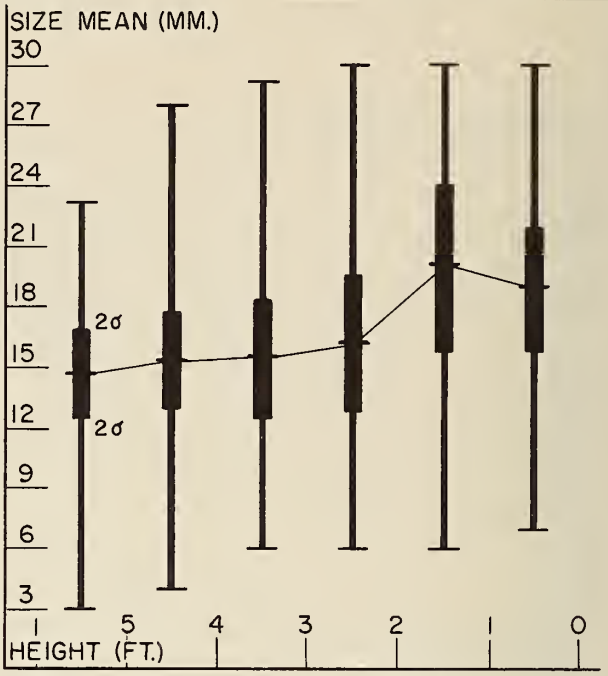

Figure 7: The range, standard deviation, and mean of *Tegula funebralis* shell size. At each depth the vertical line indicates the total range; the broad portion of the line indicates that ninety-five percent of the individuals fall within this range (2σ); the crossbar indicates the mean

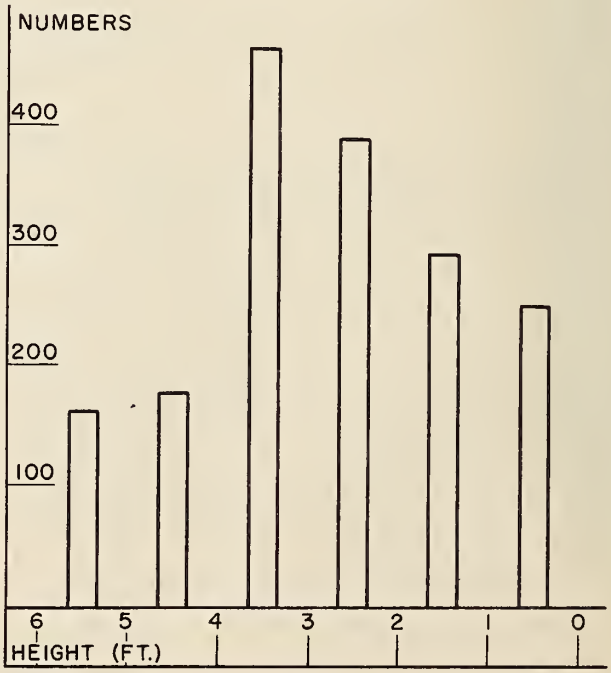

Figure 8: The number of *Tegula funebralis* per square meter found at each vertical height level above mean lower low water

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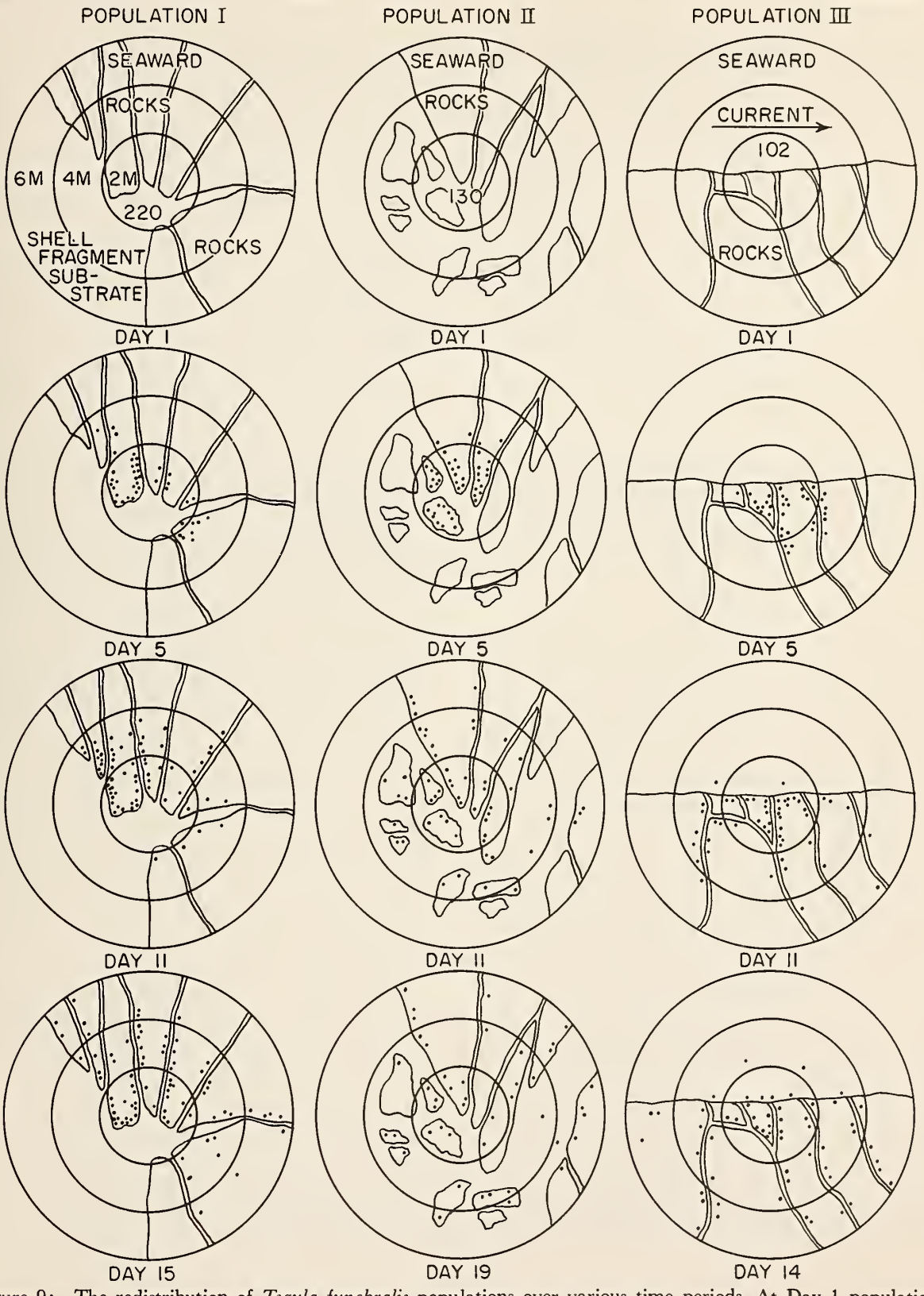

Figure 9: The redistribution of *Tegula funebralis* populations over various time periods. At Day 1 populations were placed in the center of the concentric circles